

**Relationships grow with time: a note of caution about energy expenditure-proxy correlations,
focussing on accelerometry as an example**

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Summary

Scientists studying the energy expenditure of air-breathing divers are interested in developing a more tractable technique to support their endeavour. Accelerometers instrumented to animals can return a tangible measure of those animals' activity levels, which in some situations correlates with their metabolic rate. However, I argue that reported evidence for this correlation in semi-aquatic animals while diving is not always as strong as it seems. This is because some analyses have derived a measure of activity level by calculating the *sum* of accelerometry-based values and compared those data points to measures of *summed* (total) energy expenditure. These summations mean that time (duration) has been introduced into both sides of the regression equation. This is likely to generate a correlation between body acceleration and energy expenditure even if the two variables are not mechanistically linked because time will correlate with itself. Thus a strong relationship between a summed measure of energy expenditure and a summed proxy of energy expenditure indicates only that as time passes an animal burns calories. Issues concerning summation of variables in principle extend to other potential proxies of energy expenditure, such as heart rate. I demonstrate the artefactual effect of regressing summed values with analyses of modelled data using ecologically valid parameters. Unless a summed proxy predicts total energy expenditure substantially better than does time alone there is little evidence upon which to base a claim that body acceleration is suitably predictive of metabolic rate. Clarity about the predictive power of body acceleration to estimate metabolic rate should be sought by simply presenting a graph of the relationship between these raw values.

Main text

Animals that dive underwater are fascinating, but rather hard to study. Because diving animals must breath-hold, yet are able to do so for extended periods, much research has focussed on their rates of energy expenditure while underwater (Butler & Jones 1997), which have considerable influence on their foraging durations (Halsey, Butler & Blackburn 2006). In the laboratory, or using trained animals in the field, diving animals can be taught to surface into a respirometer hood and thus their rate of oxygen consumption measured to quantify their metabolic rate (Halsey, Woakes & Butler 2003). But this technique cannot be applied to fully wild individuals. In such cases our option is to deploy data logging devices on wild individuals that measure a proxy of energy expenditure. Beginning in the 1970s, Professor Pat Butler and his lab at the University of Birmingham progressed the application of the 'heart rate technique' (initially developed by Eliassen 1960) to study the energy expenditure of diving animals (e.g. Butler & Woakes 1975). Heart rate loggers are surgically implanted and later retrieved through a capture-release-recapture protocol. Heart rate tends to correlate with metabolic rate (Boothby 1915); the harder an animal is working the faster its heart beats to support up-regulation of the cardio-respiratory system.

The technique has, and continues to be, key in elucidating the energy budgeting of diving animals, typically at the scale of at least the dive cycle (Froget *et al.* 2004) (but see also (Green *et al.* 2007)). However, as is well documented, the heart rate technique is logistically demanding (Green 2011). Two aspects that have been the chagrin of many a practitioner are the general need to implant the heart rate loggers, and even then the uncertainty that a strong electrocardiogram (ECG) will be recorded. So for a long time there has been interest in an alternative proxy for metabolic rate, which is easy to measure in wild animals. In 2005, Professor Rory Wilson, myself and others devised a plan to demonstrate that the whole-body activity of an animal can be recorded with a data logger and will relate to its metabolic rate, based on the simple premise that more energy is expended during periods of high activity (Gleiss, Wilson & Shepard 2011). Acceleration data loggers (accelerometers) had already been applied in animal research to remotely quantify behaviour (Yoda *et al.* 2001; Watanuki *et al.* 2003), demonstrating that these devices recognise changes in activity. Rory Wilson developed the metric now termed dynamic body acceleration (DBA), which can easily be derived from acceleration data and represents a broad measure of the animal's level of movement at a given moment in time – its rate of activity. We needed to demonstrate that DBA correlated with metabolic rate, but neither Rory Wilson nor I had access to laboratory animals. Once again the University of Birmingham was involved; an ongoing project there studying captive birds provided us with the opportunity. Cormorants walking on a treadmill were an unlikely model, but they allowed us to demonstrate that as the birds walked faster, not only did their metabolic rate increase but so did the acceleration of their trunk to which an accelerometer was attached (Wilson *et al.* 2006).

The accelerometry technique applied to diving animals

In the following few years, a growing number of lab-based studies were painting the encouraging picture that DBA correlated well with metabolic rate during activity in a great diversity of taxa from birds (Wilson *et al.* 2006; Green *et al.* 2009; Halsey *et al.* 2009b) and mammals (Halsey *et al.* 2008; Halsey *et al.* 2009b) to amphibians (Halsey & White 2010), fish (Clark *et al.* 2010; Gleiss *et al.* 2010) and cuttlefish (Payne *et al.* 2011).

However none of these studies investigated animals while they were diving. A relationship between energy expenditure and DBA in diving animals might be predicted because, similarly to the treadmill scenario, dives involving greater activity are associated with higher rates of energy expenditure (Halsey, Woakes & Butler 2003). In contrast to typical situations on land, however, diving involves

the complicating issues of intermittent breathing, a lack of a physiological steady state (Fedak, Pullen & Kanwisher 1988), and possibly changes in regional body temperatures affecting metabolism (Gremillet, Tuschy & Kierspel 1998; Enstipp, Grémillet & Jones 2006; Lovvorn 2007). Further possible complications associated with measuring energy expenditure during breath-hold diving are discussed in Halsey et al. (2011a). Given the value of data loggers to the study of semi-aquatic animals it was important to find out whether accelerometers could be used to estimate their energy expenditure during diving.

Cormorants again provided the model for this test of the accelerometry technique, but this time we ran the experiments at the University of British Columbia, taking advantage of their impressive 10 m-deep dive tank (Figure 1a). This super-sized laboratory environment allowed the birds to undertake repeated dives to the sort of depths they reached in the wild. They were required to surface each time into a respirometry hood (Figure 1b). Our data showed a strong correlation between total oxygen consumed by a bird each dive cycle (a dive and the subsequent surfacing period of recovery) and a summation of DBA over the same period (Halsey *et al.* 2011b [their Figure 1]). This concurred with data published some years before by Williams et al. (2004) on Weddell seals *Leptonychotes weddelli*, showing a strong relationship between total oxygen consumed and the total number of strokes performed during a dive; stroke count had been estimated from a one-axis accelerometer (Williams *et al.* 2004 [their Figure 5b]). Some recently published studies present results that also concur with these findings by demonstrating that similar relationships hold for semi-aquatic animals exhibiting a range of natural behaviours which include extensive diving. Summed DBA in combination with initial body mass and distance travelled is a strong predictor of mass change (which is closely related to total energy expenditure; Croxall 1982) in northern fur seals *Callorhinus ursinus* (Skinner *et al.* 2014). Jeanniard-du-Dot *et al.* (2016 [their Figure 2]) present strong relationships between total energy expended and summed DBA across foraging trips in both northern and Antarctic fur seals (*Callorhinus ursinus* and *Arctocephalus gazella*). The same authors followed up with a second publication on the same species indicating strong relationships between total energy expended and cumulative flipper beats (interpreted from accelerometry data) specifically during periods of diving (Jeanniard-du-Dot *et al.* 2016 [their Figure 1]), and a similar relationship was reported in northern elephant seals *Mirounga angustirostris* by Maresh *et al.* (Maresh *et al.* 2014; Maresh *et al.* 2015). Stothart *et al.* (2016 [their Figure 3a]) report as part of their findings a very strong relationship between summed DBA and mass-specific total energy expenditure during daily activities in a diving cormorant *Phalacrocorax pelagicus*.

Yet none of these findings indicate that mean DBA correlates with metabolic rate. Why?

The time trap

In each of these aforementioned analyses, both energy expenditure and DBA (or flipper strokes interpreted from accelerometry) were calculated as *summations* over the data collection period (e.g. a dive cycle or foraging bout), with one data point per animal. Thus when testing for a correlation, *total* energy expended was regressed against *total* DBA. Of course, the longer an animal is wearing an accelerometer logger the greater the summed acceleration stored on the logger and at the same time the greater the animal's total energy expenditure; both variables are increasing inexorably over time (Figure 2a). If the duration of the measurement period varies between animals, and thus between data points, in the regression, as was the case in each of the aforementioned studies, then time will correlate with itself. In other words, a correlation can exist between summed acceleration and total energy expenditure but be driven entirely by the fact that summation of the two variables has brought time into both sides of the equation (Figure 2b). In turn, this finding alone provides no evidence for a relationship between DBA and metabolic rate; interpreting that it does can be

considered as falling into the 'time trap'. This trap is not set for accelerometry alone, but is in principle awaiting any proxy measure of metabolic rate.

In our diving cormorant paper, we went on to show that there was a complete lack of relationship between *rate* of oxygen consumption and *mean* DBA (at the scales of both dives and diving bouts; Halsey *et al.* 2011b [their Figures 3 and 4]). We also made the argument that the correlation for Weddell seals reported by Williams *et al.* (2004) only arose because their analysis had fallen into the time trap. The R^2 reported for the relationship between total oxygen consumed and the number of strokes performed during a dive (0.87) was very similar to that obtained when total oxygen consumption was instead regressed against time (dive duration; $R^2 = 0.85$). (The addition of a random variable to a regression is quite likely to improve the R^2 by at least 0.02). This suggests that the number of strokes taken by the seals correlated with their total oxygen consumption only because both variables were correlated with dive duration. Furthermore, in Halsey *et al.* (2011b) we reported on a reanalysis of data presented for a relationship between rate of oxygen consumption and mean DBA in Steller sea lions *Eumetopias jubatus* (Fahlman *et al.* 2008); the one other analysis which by that time had attempted to calibrate DBA in a semi-aquatic species during diving behaviour. Our reanalysis returned an R^2 value of just 0.14 (Halsey *et al.* 2011b).

Despite consideration of the time trap being prominent in the discussion of our diving cormorant study, it appears that the warnings we offered have often been ignored (though see Stothart *et al.* 2016). Indeed, our cormorant study has been repeatedly cited as an example of the validity of the accelerometry technique for diving animals (Elliott *et al.* 2012; Skinner *et al.* 2014; Jeanniard-du-Dot *et al.* 2016). And in recent years I have refereed a number of submitted manuscripts from a host of research groups where analyses have centred around summed values of energy expenditure and DBA to test for evidence that DBA relates to metabolic rate; sometimes other referees for these manuscripts have suggested summing values as an improvement to the analysis.

There is an ever growing interest in the application of the accelerometry technique to a broadening array of species (Mosser *et al.* 2014; Williams *et al.* 2014), and a keenness to demonstrate this relatively tractable method for measuring energy expenditure in wild animals. It is therefore of paramount importance that researchers understand how easy it is to fall into the time trap, and how readily this trap springs even if the underlying measures of metabolic rate and activity levels are wholly unrelated to each other.

To impress this point, in the current article I present this concept graphically, using simulated datasets, generated in R (R Development Core Team 2011), comprising multiple independent paired measurements of ecologically valid metabolic rate and DBA recorded for a study species. This was achieved by randomly generating the model's input values (metabolic rate, DBA and logger recording duration), assuming a flat underlying distribution, within the ranges for those values reported in one of the aforementioned papers (Jeanniard-du-Dot *et al.* 2016) for northern fur seals. In my view this paper, for the reason argued in this article, concludes there is a strong relationship between energy expenditure and DBA without presenting sufficient evidence. Specifically, the model presented in the current study has the same number of data points (animals) to that of Jeanniard-du-Dot *et al.* (2016), and a similar mean and spread of recording durations associated with those data points. The range of metabolic rates and the range of mean DBA values were also very similar to those presented in that empirical study. Within this framework, the random generation of metabolic rate and mean DBA values simulated the sampling of two variables that are unrelated. Modelled metabolic rate was then summed to calculate total energy expenditure, i.e. it was calculated as the product of metabolic rate and recording duration (time). Summed DBA was calculated as the product of mean DBA and time. Finally, the R^2 values were calculated for the linear

regression of metabolic rate against mean DBA, and total energy expenditure against summed DBA. 10 000 iterations of the model were run.

As would be expected for two randomly generated variables, the relationship between metabolic rate and mean DBA was typically negligible (Figure 3a and c, and Figure 4a). Mean $R^2 \pm 1$ standard deviation was 0.10 ± 0.12 . The relationship between total energy expenditure and summed DBA was most commonly of medium strength (Figure 3b). However, it varied around this mean value encompassing almost the full range of possible R^2 values (0 to 1; Figure 4b). Mean $R^2 \pm 1$ standard deviation for this relationship was 0.50 ± 0.20 . The mean R^2 value is therefore improved by the inclusion of time to both sides of the regression equation by on average 0.40 (Figure 3a v. Figure 3b). The frequency distribution of R^2 values for the relationship between total energy expenditure and summed DBA was Gaussian, indicating that in around half of the simulations R^2 was even higher than 0.5. Thus the chances of generating a relationship returning an R^2 considerably higher than 0.5 despite metabolic rate and mean DBA being entirely unrelated is substantial (Figure 3d).

Concluding thoughts

The allure of diving animals is unabated; rightly so researchers continue to be captivated by their breath-holding feats and there is much still to learn (Elsner 2015). Despite the development of the heart rate technique (Green *et al.* 2007) and other methods such as the doubly-labelled water technique (Shaffer 2011), obtaining accurate estimates of energy expenditure in submerged divers is still laden with difficulties (Butler *et al.* 2004; Halsey 2011). It is therefore understandable that researchers want the accelerometry technique to work with such creatures. And there is evidence that, at least for sea turtles, it does. Both Enstipp *et al.* (2011) and Halsey *et al.* (2011a) reported strong lab-derived relationships between metabolic rate and mean DBA during diving bouts in green turtles *Chelonia mydas*.

However, given that the models presented in the current article demonstrate how the time trap can produce good relationships between energy expenditure and DBA when the two variables are not mechanistically linked, the conclusion from the literature thus far must be that there is a lack of compelling evidence for a metabolic rate-mean DBA relationship in any other taxon while diving. And this is supported by a string of papers on pinnipeds broadly concluding that there is little evidence the accelerometry technique works on these species when they are at sea (Dalton, Rosen & Trites 2014; Skinner *et al.* 2014; Volpov *et al.* 2015; Volpov *et al.* In Press); see also Rosen *et al.* (2016). Finally, while there is some evidence that in seabirds the relationship can arise across a broad array of behaviours that include diving, it is unclear whether the relationship holds during diving periods alone (Elliott *et al.* 2012; Stothart *et al.* 2016).

Halsey *et al.* (2011a) in particular discuss possible reasons why there is this contrasting success for the accelerometry technique between turtles and other species (see also Elliott *et al.* 2012; Volpov *et al.* In Press). For many diving animals their movements may be damped while submerged resulting in activity while at the surface having an unrepresentatively large effect on DBA, exacerbated by wave action; however, most of the green turtle's body is submerged when it is at the water surface (Halsey *et al.* 2011a). Heat lost during dives can also uncouple energy expenditure from body movement (Gremillet, Tuschy & Kierspel 1998; Enstipp, Grémillet & Jones 2006), but the metabolic rate of green turtles is not thermally dependent at the water temperatures they experience in the wild (Southwood *et al.* 2006). In some scenarios and species, digestion, gliding behaviour and buoyancy may also disrupt the potential relationship between DBA and metabolic rate (Volpov *et al.* In Press).

In time it might be shown that, at least under certain conditions, the metabolic rate-mean DBA relationship is also present in species where thus far the evidence for this correlation is poor. Accounting for metabolic suppression during dives (Stothart *et al.* 2016) or the confounding influence of wave action on the body during surface periods (Elliott *et al.* 2012), may offer some routes to uncovering relationships currently hidden. Otherwise, perhaps higher computational analyses of acceleration data, for example including gyroscope or magnetometry data to discriminate linear from rotational motions (López *et al.* 2016; Ware *et al.* 2016) will characterise diving behaviour sufficiently well such that it can be effectively related to metabolic rate, so long as a sufficient portion of metabolic rate is explained by body movements (Halsey, Shepard & Wilson 2011; Elliott 2016). Other possibilities include the addition of cameras to clarify how acceleration relates to behaviour details (Cade *et al.*), or combining heart rate and accelerometry measures (Bishop *et al.* 2015), or coupling the accelerometry analysis with biomechanical modelling (Elliott 2016).

An argument might be made that summing DBA values, while inappropriate for assessing whether higher activity rates are related to a higher metabolic rate, might nevertheless be an effective way to estimate the energy an animal has expended over a given period of time such as a dive or diving bout. After all, summed DBA incorporates both duration and degree of activity, both of which might be good predictors of total energy expenditure. This supposition can only be confirmed, however, by comparing the strength of the relationship with that of the correlation between total energy expenditure and time (alone). In the aforementioned diving Weddell seal example (Williams *et al.* 2004), as discussed earlier this comparison did not provide evidence for the predictive power of accelerometry. Indeed, considering flipper beats as the energy expenditure proxy provides a clear image of the mistake made in interpreting cumulative values as evidence for a relationship between rates. The seal's flippers are somewhat analogous to a ticking clock; tick-tock, tick-tock – the beats of the flippers count the accumulation of passing time. And, of course, the model outputs in the present article support this argument, illustrating how a relationship between the summations can exist without any underlying relationship between the rates. The simplest way to separate out the complicating and confounding effects of time when assessing the efficacy of the acceleration technique as a predictor of energy expenditure is to leave time out of the equation.

In the present article I do not argue that the accelerometry technique is a poor method for estimating rates of energy expenditure in wild animals; as with all methods, it has its limitations (Halsey, Shepard & Wilson 2011) yet in many scenarios its effectiveness has been demonstrated (Wilson *et al.* 2013; Brodie *et al.* 2016). I also do not argue that accelerometry for estimating rates of energy expenditure is inappropriate for diving animals in general; it has been shown to calibrate in turtles (Enstipp *et al.* 2011; Halsey *et al.* 2011a) and there is also an argument that, at least within individuals, changes in mean DBA may provide qualitative insight into changes in metabolic rate (Halsey *et al.* 2009a; Green 2011; Halsey, Shepard & Wilson 2011). Nor do I even argue that particular species or situations are definitely unsuitable for the technique. Rather, I have suggested that certain studies claiming strong evidence that the technique works for particular species have overstepped the mark, because the time trap has limited the insight of their correlative analyses.

When we have gathered data that we believe indicate a relationship between metabolic rate and mean DBA or the mean of any other proxy, for the sake of full disclosure and clarity we should present this key finding as a straightforward plot of the raw values.

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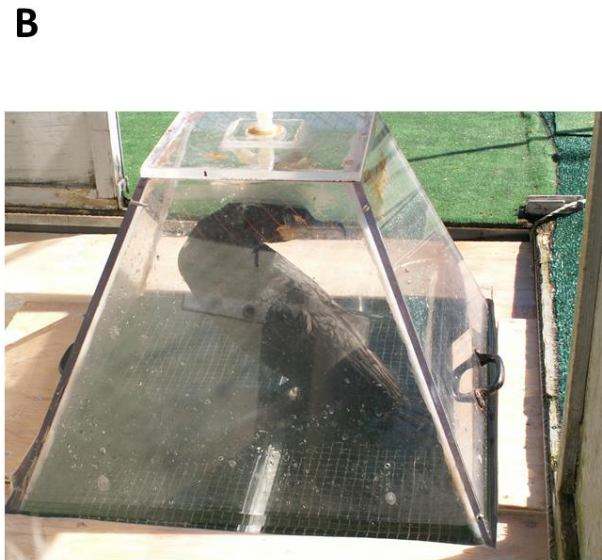


Figure 1. (a) The 10-m dive tank at the University of British Columbia. (My colleague Craig White can just be made out standing at the top, in front of the viewing hut). (b) The double-crested cormorants had to resurface after each dive into a respirometry hood, in order that their rates of respiratory gas exchange could be measured. In this photograph, the cormorant has been placed within the hood prior to the start of the experiment. Upon commencement of the experiment, the netting that the bird is standing on falls away to allow the bird access to the water below.

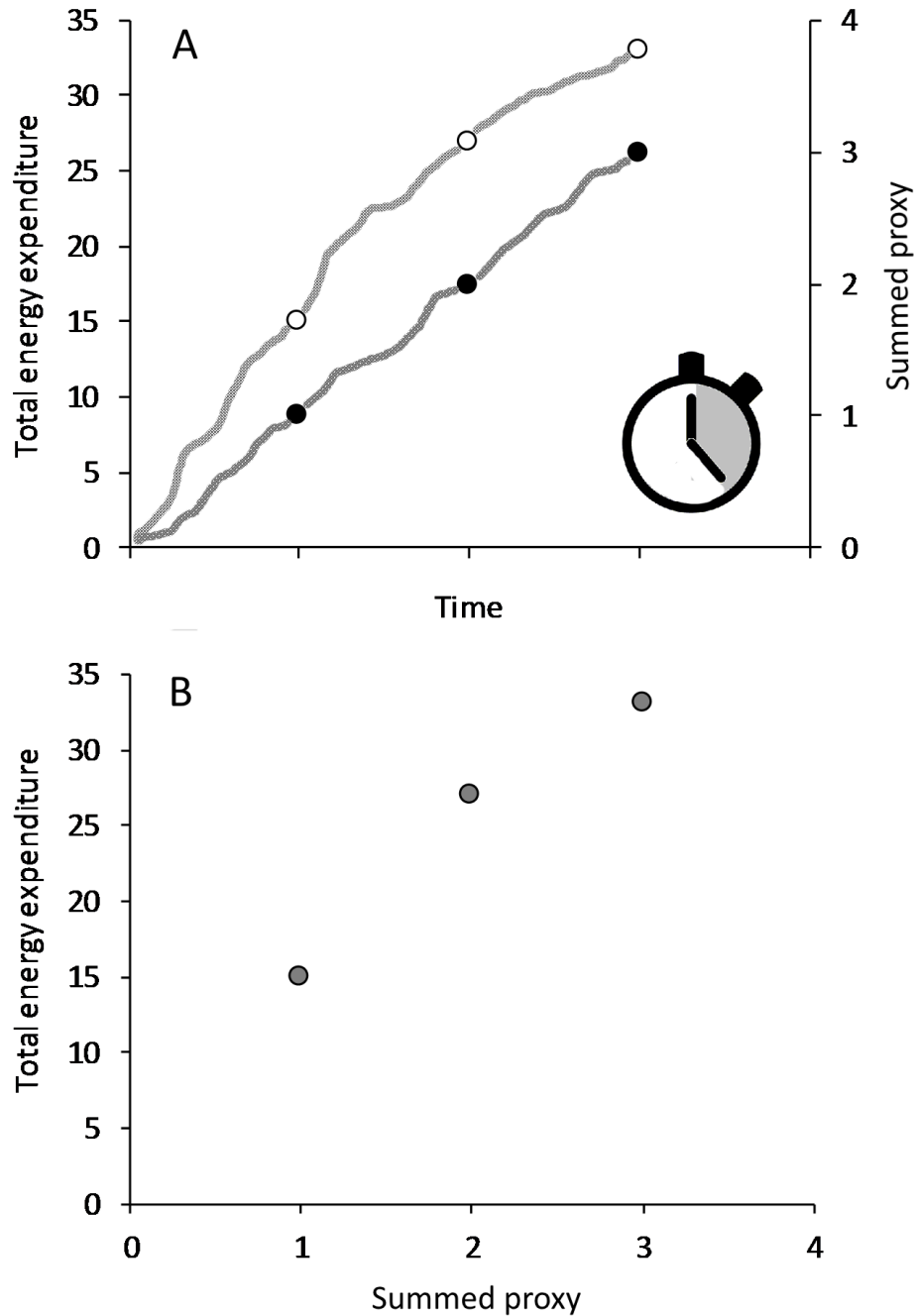
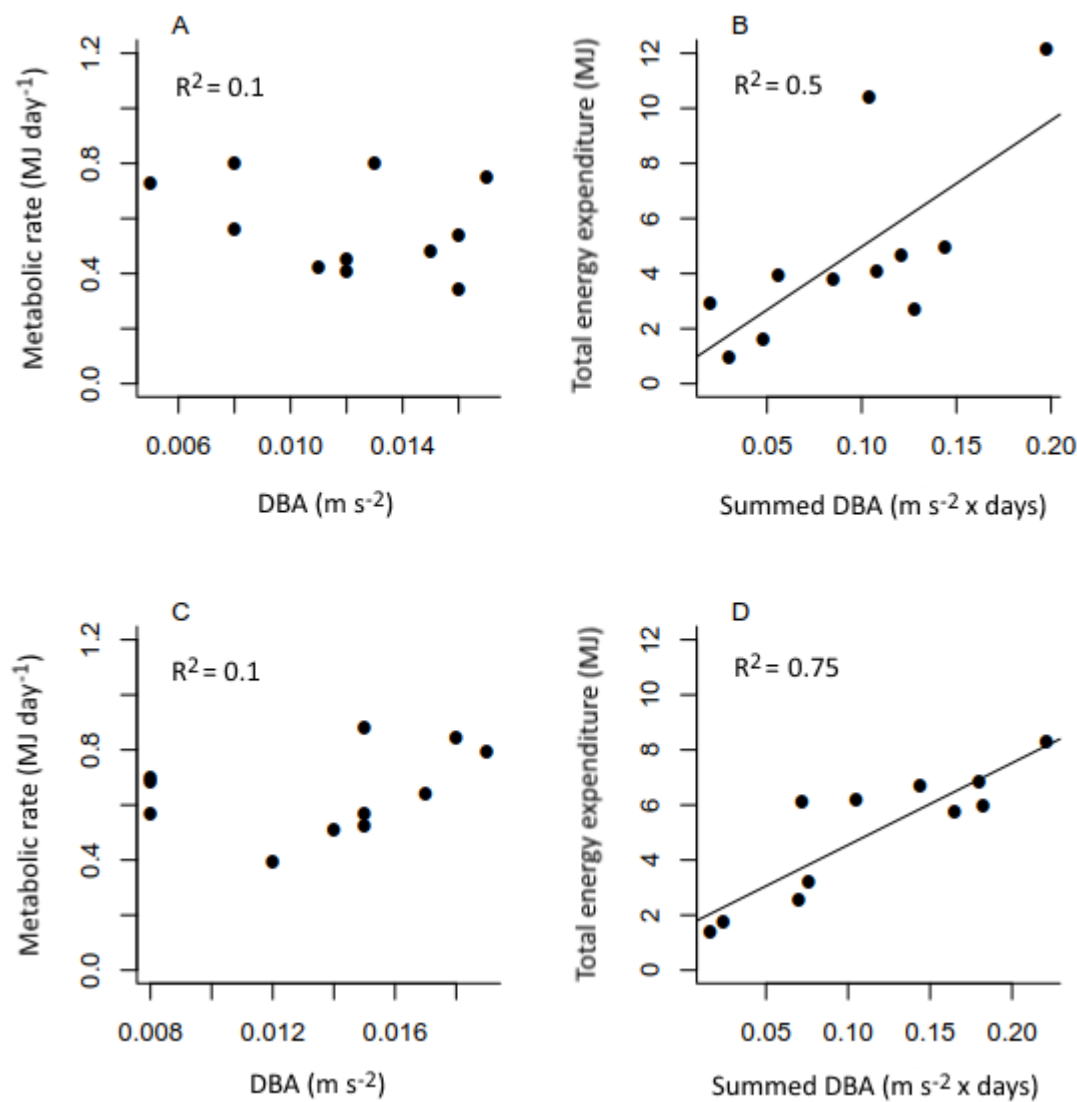


Figure 2. As the time that an experiment has been underway increases, cumulative measures recorded during that experiment inevitably increase in size. (a) The total energy expenditure of an animal in the field will inexorably increase as time passes (upper line), as will summed measures of the proxy recorded on the data logger instrumented to the animal (lower line). I.e. both these variables innately correlate with time. For the same animal or different animals, it is therefore very likely that correlating coupled measures of total energy expenditure (open circles) against a totalled value of the measured proxy (closed circles) taken from distinctly different time points will (b) result in a strong relationship, and this can be driven simply by the relationship between both variables and time.



292 Figure 3. Examples of the simulated relationships between energy expenditure and dynamic body
293 acceleration (DBA) produced by the model, where R^2 increases considerably when these two
294 variables are multiplied by time. (a) and (c) Relationships between metabolic rate (MJ d⁻¹) and mean
295 DBA, where the values for each variable were randomly generated within pre-set upper and lower
296 bounds. (b) and (d) Relationships between the product of metabolic rate and time (total energy
297 expenditure), and the product of DBA and time (summed DBA), where the values of metabolic rate
298 and mean DBA were those generated to create the relationships presented in (a) and (c)
299 respectively, and the values of time associated with each data point were unique and ranged
300 between pre-set upper and lower bounds. See main text for further details. In (a) and (b) the R^2
301 values for each relationship (a: $R^2 = 0.10$; b: $R^2 = 0.50$) are very close to the mean and modal R^2
302 values from 10 000 iterations of the model. Panels (c) and (d) show a more extreme scenario but one
303 that still occurred quite frequently, in which R^2 for (a) the relationship between metabolic rate and
304 mean DBA was again 0.10 however (b) the R^2 for the relationship between total energy expenditure
305 and time, and summed DBA, was 0.75.

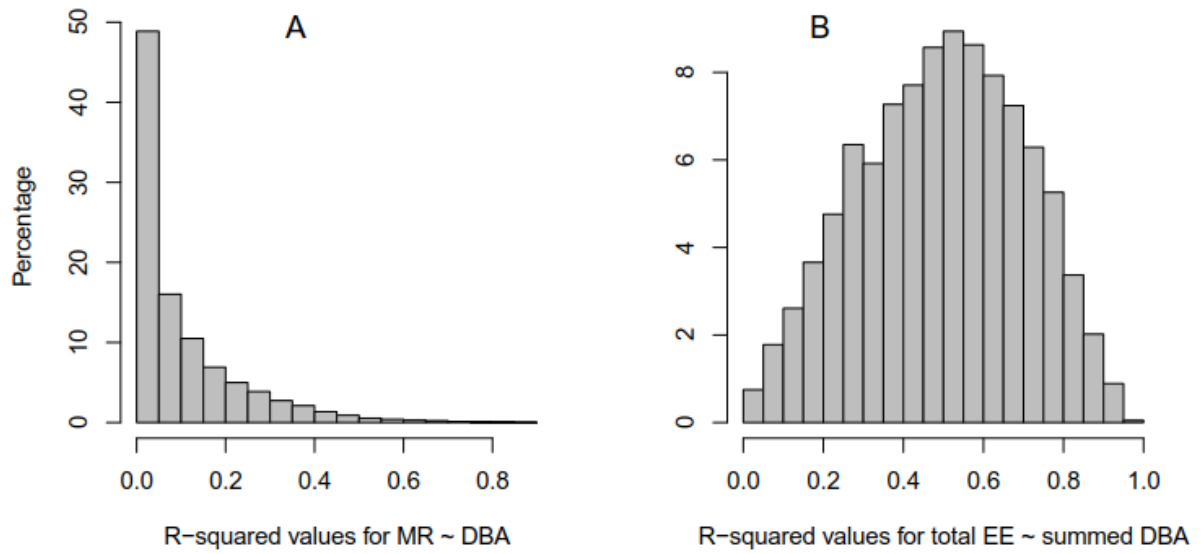


Figure 4. The percentages of binned R^2 values between 0 and 1 for 10 000 iterations of a modelled linear relationship between (a) metabolic rate (MR) and mean dynamic body acceleration (DBA), and (b) summed MR (total energy expenditure; total EE), and summed DBA. See the main text for details.

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